

Almond Board of California Annual Report - 2001-02

Project Title: Almond Variety Development

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Objectives:

Develop (1) improved pollinizers for *Nonpareil*, and ultimately, (2) replacement varieties for *Nonpareil* and its pollenizers that possess self-fertility, improved disease and insect resistance.

- A. Finalize and oversee the release 'UCD 13-1' -the pollinizer for early *Nonpareil* bloom. Establish verified true-to-type sources of virus free bud wood for 'UCD 13-1' , *Nickels* (UCD 1-82 -a hybrid rootstock for almond with improved disease resistance) and the low Noninfectious Bud-failure (BF) *Carmel* sources.
- B. Breed new selections, and test breeding lines for resistance to key pests (particularly Navel Orangeworm) and diseases (particularly Anthracnose), and characterize their cross-compatibility groups using molecular as well as field tests. Continue to develop genetic alternatives to chemical control of important almond diseases, including shot-hole, aflatoxin causing *Aspergillus flavus*, *Monilinia* hull rots and flower blights, and Noninfectious Bud-failure. Continue to evaluate advanced selections 2-19E and 1-87 for productivity and disease resistance.
- C. Develop a model for the classification of cropping potential in almond. Test this model for predicting mature cropping potential of new varieties based on early tree performance.

Summary:

The recent releases to California growers of 'Winters' as a productive early 'Nonpareil' bloom pollinizer, and FPMS#1, a low Bud-failure 'Carmel' clone covering the later 'Nonpareil' bloom have achieved the initial breeding goals of effective pollinizers for 'Nonpareil'. The release of the 'Nickels' rootstock, along with advanced field testing of low Bud-failure 'Nonpareil' clonal sources, the NOW resistant selections such as 36-52 and the disease resistant selections such as 2-19E demonstrate continued progress towards developing resistant varieties with high cropping potential. Specific strategies and research findings for programs to develop insect resistance and for characterizing tree architecture as a component of cropping potential are highlighted in this report.

Commercial almond production is threatened by continuing losses of traditional insecticides, fungicides and insect pollinators. New domestic and international markets developed over several years of good production are lost when poor pollination conditions result in insufficient crop to meet established demand. Similarly, unique opportunities now exist to expand market demand by optimizing the phytonutrient benefits of almond in new California almond varieties while minimizing potential health and marketing risks such as aflatoxins, kernel cyanoglucosides and allergens. Thus, continued profitability of this industry relies upon dependable and quality production with reduced inputs. Breeding success depends upon locating sources of needed germplasm, the efficient selection and transfer of desired genes through controlled crosses, and the generation of large numbers of progeny from controlled crosses to ensure recovery of the rare, horticulturally superior individuals.

A. Finalize release as new varieties and establish verified true-to-type sources of virus free bud wood.

Applications and associated paperwork for the patenting and release of UCD 13-1 has been submitted to the UCD patent office. Patenting and release of the *Nickels* rootstock has been completed. Clonal sources of the variety *Carmel* that have been selected from long-term regional testing as having low Bud-failure potential have completed FPMS registration and certification and have been released to the industry as unpatented selections.

Nursery budwood sources for all released selections have now been tested and shown to be free of known viruses, and have been established in FPMS clean (quarantined) orchards for distribution to nurseries as Foundation Stock. The trueness-to-type for these FPMS planted selections will continue to be tested in 2001 as field evaluations of tree growth and

nut characteristics, and when necessary, molecular fingerprinting. Testing of *Winters* pollen cross-compatibility with *Nonpareil* and *Carmel* has shown full cross-compatibility based on molecular S-allele

fingerprinting. *Winters* bloom continues to show excellent overlap with that of *Nonpareil* and this variety continued to be the highest producer in the Butte RVT (Fig. 1). More moderate production in the Delta and Kern RVT can be attributed to irrigation problems (Delta) and crop loss from *Alternaria* infections (Kern).

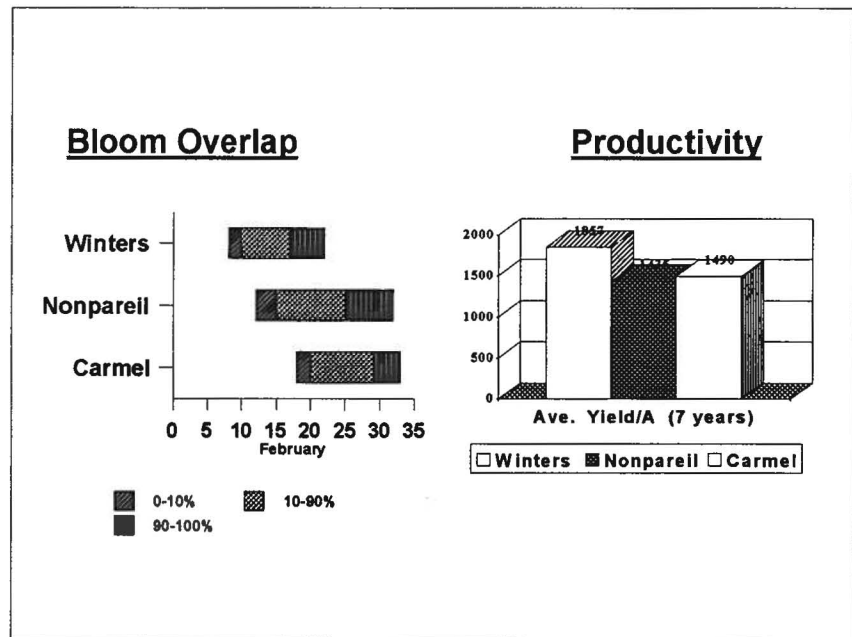


Figure 1. Average performance of *Winters* almond at the Butte RVT from 1995 to 2001.

B. Breed new selections, and test breeding lines for resistance to key pests and diseases. Even with well-matched parents, the probability of a seedling progeny inheriting the best genes for the multitude of desired traits including self-compatibility, high nut quality, and maximum yield potential, and disease/pest resistance is very low. To increase the likelihood of breeding such an elite individual, very large populations of seedlings from controlled crosses have been generated. In addition, since the best crossing combinations can only be verified by evaluating their progeny, a large number of different crossing combinations have been employed. Controlled crosses in 2001 have achieved the goal of

3,000 seedlings from over 20 different crossing combinations. This continued success in achieving high returns from controlled crosses under often difficult February field conditions had fed a consistent expansion in overall breeding program size (Fig. 2) leading to increasing efforts to crop evaluation as seedling trees come into production (typically after 3-4 years of growth).

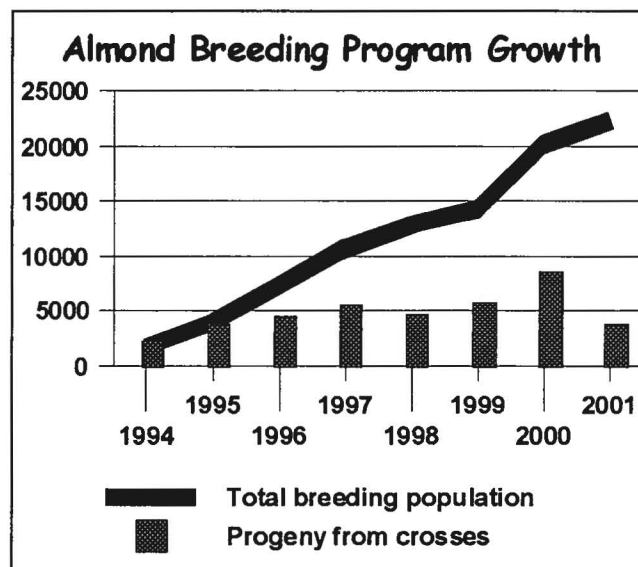


Figure 2. Almond breeding population growth over the last 8 years.

Approximately 50% of controlled crosses in 2001 have been directed towards pest (particularly NOW) and disease (particularly *Aspergillus* spp.) resistance. Components associated with NOW resistance include hull, shell and kernel structure and biochemical composition. Our present understanding indicates that the most durable resistance to NOW (and ant) damage results from the development of an impenetrable shell structure. Most European and Asian cultivars possess a thick shell derived from the lignification of the fruit endocarp, which protects the kernel from insect damage and disease infection. The endocarp often accounts for over 60% of total nut dry-weight resulting in a low kernel-to-nut mass ratio (crack-out), greater mechanical difficulty in shelling kernels, and greater damage to kernel meats during shelling. The utilization of high-yielding cultivars combined with high-input orchard management practices has made California a leading producer of almonds. Shells of high yielding California cultivars are thin and only moderately lignified with crack-out ratios from 45% to 75%. Lower shell mass is associated with greater damage during nut

development from the hemipterous insects lygus bug (*Lygus hesperus* Knight) and leaffooted bugs (*Leptoglossus clypealis*), and at nut maturity from the more destructive lepidopterous insects navel orangeworm (*Amyelois transitella* Walker) and to a lesser extent peach twig borer (*Anarsia lineatella* Zeller). Insect damage to the mature seedcoat tissue, which normally acts as a barrier to fungal infection, results in a greater incidence of kernel infections by aflatoxin-causing *Aspergillus* Speare sp.

The almond fruit hull, a leathery and tannic mesocarp derived tissue, protects the immature kernel from insects and disease. At nut maturity, however, the hull dries and splits, leaving the shell as the remaining barrier to insect attack. Over 90% of insect damage to California almonds occurs following hull split, through cracks in the endocarp. The integrity of the mature shell varies with genotype, with the proportion of intact nuts ranging from 90% sealed and higher in semi-hard-shelled cultivars such as 'Mission', to as low as 20% sealed in soft 'paper-shelled' cultivars such as 'Merced'. 'Nonpareil', the major California almond cultivar which accounts for approximately 44% of total production, has a thin paper shell with a crack-out ratio of ~ 65% and average proportion of well-sealed nuts of approximately 60%.

Cultural practices, including crop load, scheduling of fertilizer and irrigation application, and rootstock selection, influence the final extent of endocarp fracturing in susceptible cultivars of almond and peach [(*Prunus persica* (L.) Batsch (subgenus *Amygdalus*)]. Endocarp fracturing in peach, commonly known as split-pits, is believed to occur when rapid mesocarp expansion leads to separation or fracturing of the more rigid endocarp at the ventral suture line, as this is one of the last areas to lignify during fruit development. Cultural practices associated with increased levels of split-pits in peach are also associated with accelerated mesocarp expansion. Almond fruit, while structurally similar to peach, lack

a rapid mesocarp expansion after endocarp lignification. The mature almond endocarp, unlike the more uniform and highly-lignified peach endocarp, consists of a partially lignified central layer containing the vascular bundles sandwiched between a more highly lignified inner layer and an outer layer with moderate lignification. In addition, while almond shell fractures occur at the suture, they are usually adjacent and parallel to the suture line.

The continuing loss of chemical insecticides traditionally used to control almond pests has made natural barriers to insects and disease, such as well-sealed shells, attractive alternatives. The objective of this study was to characterize shell seal breakdown in 'Nonpareil' almond and assess opportunities for its cultural and genetic manipulation.

Frequency and location of shell fractures. Samples were collected from 8-year-old 'Nonpareil' almond trees growing under standard commercial conditions in regional cultivar trials at Chico, Calif. (northern Sacramento Valley), Winters, Calif. (southern Sacramento Valley) and Manteca, Calif. (northern San Joaquin Valley). Five hundred nuts (including endocarp, seed and occasionally attached hulls) were randomly collected ~185 d after flowering (DAF) from the orchard floor at the Chico plot following mechanical-shaker harvesting. Samples were collected randomly both before and following mechanical harvesting of trees at the Winters (180 DAF) and Manteca (175 DAF) plots. Nuts were examined visually, and when necessary, under a stereomicroscope, and scored for the presence and location of shell fractures. Fractures along the ventral vascular bundles located adjacent to and parallel with the suture, were characterized further by the condition of the adjacent ovule. The almond fruit has a single ovary containing two functional ovules with funicular attachments on either side of the suture line. One ovule, designated the

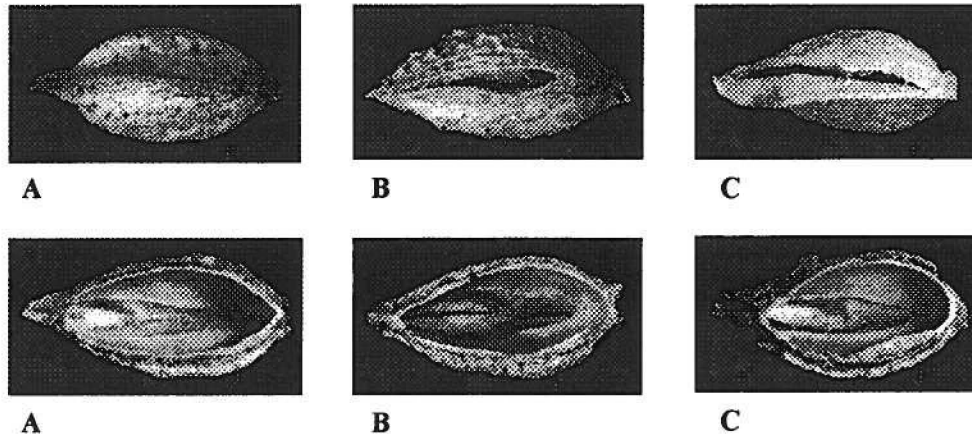


Figure 3. Shell seal in 'Nonpareil' almonds showing: (top) the ventral side of whole nuts, and (bottom) interior view following removal of kernel and dorsal portion of shell exposing funiculi sites at distal, styler end of fruit (A =sealed shell, B =split at suture line, and C =split adjacent to suture line along the thickly lignified suture wing and through the funiculus and ventral vascular bundles).

secondary ovule, usually aborts in 'Nonpareil' and other California almonds.

Nuts with fractured shells were observed in 72% of the mechanically harvested almonds sampled in 1999 (Table 1). Fractures occurred as a splitting along the ventral side of the shell near the suture. Splitting at the suture line occurred in only one of the 500 nuts sampled. Shell splits in the remaining nuts occurred adjacent and parallel to the suture at the base of the thickly lignified shell wing commonly found in 'Nonpareil' and other California cultivars (Fig. 3). Splits ranged in width from < 1 mm, to up to 1 cm, and up to several

centimeters in length. Most shell splitting occurred along the distal portion of the suture near the funiculus (Fig. 3). The outer layer of the 'Nonpareil' shell was soft and papery, and easily flaked away from the only partially lignified middle layer containing the vascular bundles. The inner, more highly lignified shell layer was the most resistant to splitting. There was no difference in the occurrence of embryo abortion between the two funiculi positions within the fruit (data not presented). The specific site of shell split initiations, however, could be identified in 294 of the 361 fractured nuts sampled in the first year of testing and the majority of such fractures (78.2%) were located along the secondary funiculus leading to the aborted or secondary ovule (Table 1). This frequency was significantly different from an assumption of equal probabilities for the two funiculi. Similar observations were made for samples collected in year 2 from Manteca and Winters, Calif. (Table 1). The proportion of mechanically harvested nuts showing split shells was 51% for both locations. When the nuts were hand-harvested from the trees just prior to mechanical harvesting, a 40% reduction in the proportion of damaged shells was observed. As in 1999, splits at the suture line were rare (3 in 337 fruit), with the majority (74% to 89%) of remaining splits occurring at the secondary (aborted) funiculus (Table 1, Fig. 3). Ratios were again significantly different ($P < 0.005$) from an assumption of equal probabilities of splitting at the two funiculi.

Structural integrity of developing endocarp. Samples of eight fruit each were collected at approximately 50 DAF from four separate trees at the Manteca regional almond cultivar trial. Sample fruit were cut longitudinally at right angles to the suture line, and the strength of the inner endocarp tissue at 10, 45, 90, 135, 170, 190, 225, 270, 315, and 350° relative to the peduncle (Fig. 1) was measured using a Mechanical Force Gauge (Model L-10-M, U.C. Hunter Spring) (Ametek, Hatfield, Pa.) with a 1 mm flat probe. Measurement was on the tangential plane offset 10° from the suture line so as to pass through the secondary

funiculus (Fig. 1). Endocarp strength was measured similarly in a cross-sectional plane at the points of funiculi attachment approximately midway between the fruit mid-section and the distal, styler fruit tip, (Fig. 1). Measurements were taken at 0, 10, 45, 90, 135, 180, 225, 270, 315, and 350° relative to the suture line. For consistency, the site of funiculus attachment to the secondary (aborted) ovule was chosen as the 10° measurement position (Fig. 1), with measurements continuing in a circular pattern culminating in the position of primary (nonaborted) ovule attachment (350°) with the suture line at 0°. Fruit cross-sections were examined similarly from 60 to 150 DAF following placement of the cut fruit surfaces in 10% toluidine blue stain for 10 minutes to stain lignin-containing cells in the developing fruit.

Immature nuts sampled at 50 DAF from the Manteca orchard showed a relatively firm inner-endocarp wall, though with significantly reduced strength near the peduncle (350°) and more extensively, at the distal, ventral suture (from 90 to 180° in the longitudinal sections in Fig. 1, and Tables 2 and 3). Measurements in the cross-sectional plane also showed uniform firmness for the inner-endocarp wall but with significantly reduced strength at the two funiculi (10 and 350°) and a significantly greater strength at the suture line (0°) (Tables 2 and 3). Endocarp wall strength at the degenerating, secondary funiculus was slightly though significantly less than at the functional primary funiculus. The position x tree interaction for cross-section data (Table 3) was also significant, presumably due to small differences in nut maturity among trees. Similar patterns of endocarp strength were observed for fruit harvested at 54 DAF from Winters, Calif. (data not presented). Toluidine blue staining of fruit cross sections at this stage of development showed lignification occurring throughout the endocarp but being more intense at the inner endocarp and at the ventral suture region including the vascular strands of the funiculi and ventral vascular bundles. By 130 DAF, lignin was well-distributed within the 'Nonpareil' endocarp though with apparent discontinuities in lignin density at the funiculi and at the suture line.

Frequency and location of kernel damage by leaffooted bug. One hundred 'Nonpareil' fruit demonstrating external fruit wounding and gum formation from leaffooted bug feeding were collected from an organic orchard in Madera, Calif. ~ 60 DAF, during the period of endocarp lignification. Fruit were dissected and scored for both the incidence of internal damage to the kernel as well as its location using the same coordinates as in the endocarp strength testing (Fig. 1). Kernel damage was considered to have occurred when both physical puncturing of the kernel and seed coat by the insect's stylet and associated tissue browning were observed.

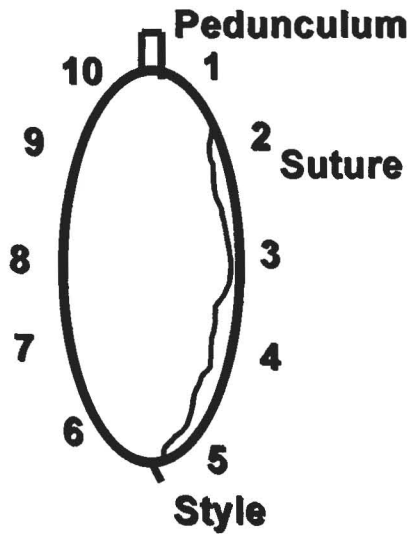
Data was analyzed using the StatView statistical analysis program (SAS Inst., Inc., 1998). Differences in the site of endocarp failure (primary vs. secondary funiculus) were tested by chi-square analysis. Positional effects on the strength of the developing endocarp were tested by analysis of variance (ANOVA) and means separated by Fisher's least significant difference (LSD).

Leaffooted bug damage to immature fruit at 60 DAF occurred as a physical wounding of the fruit surface followed by a distinct gum exudation. Feeding damage was observed on all fruit surfaces but was more common on the distal portions of the fruit, particularly near

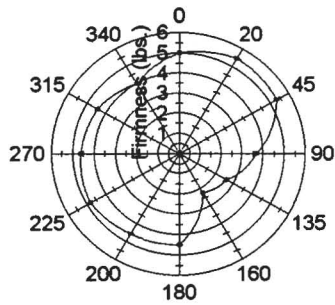
Fig. 4. Longitudinal and cross-sectional distributions of: (top) force required to puncture the inner endocarp of 'Nonpareil' almond at 50 DAF, and (bottom) kernel damage by leaffooted bug at 60 DAF. (Dashed line at 'x' identifies plane of cross-section; dotted line at 'y' identifies plane of tangential longitudinal section of tested almond fruit).

Firmness in almond fruits

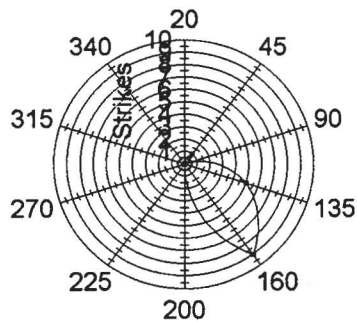
Longitude



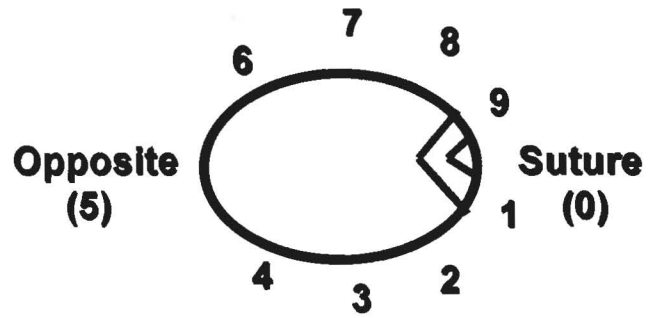
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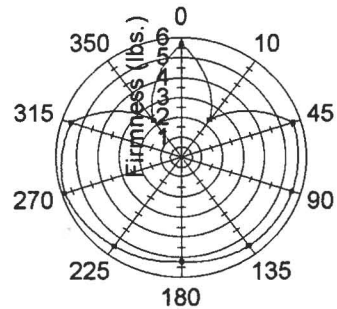
Lygus-Longit.



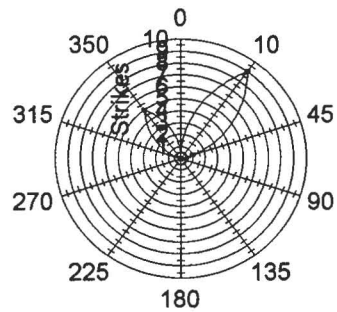
Transverse



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Lygus-Transv



the ventral suture. Leaffooted bug damage extending to the developing kernel was found in only 21 of the 100 damaged fruit dissected (Table 4). While feeding damage at the hull surface was distributed widely, feeding damage to the developing kernel was limited to the ventral suture area and occurred almost entirely at the secondary funiculus (Table 4 and Fig. 4). At this stage of nut development, the inner endocarp had a semi-hard eggshell-like appearance with moderate levels of lignification as observed as a dense blue-violet staining following 10 min immersion in toluidine blue. Damaged kernels usually continued to develop though often with tissue shriveling at the wound site. Feeding damage before the kernel had reached full size often resulted in abortion of the ovary and consequent nut drop by 100 DAF.

In summary, shell splitting in almond is highly localized in its occurrence near the endocarp ventral suture. The presence of external shell splitting adjacent to, rather than at the suture line in almond could result from initial failure of the suture seal at the more highly lignified inner endocarp (as predicted by the peach split-pit model) with external splitting occurring obliquely through the funiculus and ventral vascular bundles following the path of least structural resistance, (given the soft-shelled nature of almond and the relatively massive winged structures at the suture). However, virtually all shell splits in the 'Nonpareil' nuts examined originated near the funiculi, rather than the endocarp suture line, indicating a distinct mechanism for soft-shelled almonds. The close proximity of funicular and ventral vascular bundles in 'Nonpareil' makes this section particularly vulnerable to fracturing in response to physical strains during fruit development. The preponderance of splitting at the site of the secondary funiculus and associated vascular bundle (Table 1 and Fig. 3), as well as the reduced strength of the inner endocarp at this site as early as 50 DAF (Table 2 and Fig. 4), indicate that developmental as well as structural forces are involved. Since abortion of one of the two ovules in 'Nonpareil' almond occurs soon after anthesis and may be

initiated before flower fertilization, the site of final shell splitting appears to be largely determined very early in fruit development. Interestingly, an early but obscure 1932 study of split-pits in peach observed that callus formation at the site of the aborted secondary ovule and funiculus predisposed that endocarp tissue to later splitting. The friable nature and reduced lignification observed in our examination of this tissue support such an inherent weakness, presumably resulting from its altered tissue development. If confirmed in other almond cultivars, the recognition of such an ontogenetic "Achilles" heel could prove useful for the genetic and cultural manipulation of shell seal quality. For example, genotypes with shell structures similar to 'Nonpareil' that have lower rates of shell splitting are known. Identification of the mechanism for this low shell-split trait (for example, timing of secondary ovule abortion or increased separation between funicular and ventral vascular bundles), could lead to greater selection efficiencies for this trait. It is a desirable cultivar trait to have one of the two ovules abort early since development of both ovules results in twin, and often deformed kernels. Susceptibility to kernel meat damage by the leaffooted bug also varies with genotype and appears to result from different endocarp development and lignification rates. In 'Nonpareil', all damage to the immature but fully formed kernel occurred along the ventral suture. Insect damage to fully formed kernels is a more serious problem to processors as the consequent nut deformities predispose the kernels to disease and have to be sorted out. Most damage occurred close to the secondary funiculus, which has been shown to be the weakest tissue in the developing endocarp. Leaffooted bug preference for this region could also result from changes in vascular development associated with the ovule abortion. Changes in vascular tissue development in the endocarp could result similarly in regional differences in endocarp desiccation and so integrity at hull-split.

Opportunities for cultural manipulation are demonstrated by the 40% reduction in shell splits for nuts that were harvested by hand rather than mechanically. This finding suggests

that while the developing endocarp may have internal structural weaknesses, external (i.e., mechanical shaker) forces may ultimately cause more damage than internal forces. Unlike peach, the almond mesocarp or hull is only loosely attached to the endocarp and so exerts less force on the shell during hull desiccation (hull-split). Similarly, while peach split-pits can often be identified in immature fruit, no instance of endocarp splitting was observed in almond until fruit desiccation and the associated hull split. The most serious damage to the almond crop occurs between the time of hull split and harvest. Since the insect pests involved, navel orangeworm and to a lesser extent ants, gain access to the nut meat only through pre-existing fractures in the shell, any reduction in the extent and duration of post-shaker kernel damage could reduce crop loss. Promising cultural practices to reduce insect feeding include the reduction of the time (typically 5 to 15 d) between mechanical shaking and harvest of the nuts from the orchard floor. Alternatively, mechanical shaking directly to catch frames as with prunes (*Prunus x domestica* L.) and other stone-fruits, could considerably reduce nut vulnerability to post hull-split insect damage.

The clear association of the site of the secondary ovule/funiculus with shell-splitting in 'Nonpareil' almond has important pest management implications since 'Nonpareil' accounts for almost 50% of current U.S. production. This model is presently being tested for other California and Spanish cultivars to determine its consistency among genotypes and to better understand the crucial development processes.

Table 1. Proportion of Nonpareil almond nuts showing split shells, and location of splits for affected shells. Percentages are in parentheses

Year	Source	Harvest	Sample size	Split nuts	Scorable nuts	Location of shell split						χ^2
						Suture Line	Developing ovule	Abortive (2°) ovule				
1999	Chico	Mechanical	500	361 (72.2)	294	1 (0.3)	63 (21.4)	230 (78.2)				<0.005
2000	Manteca	Hand	240	67 (27.9)	63	0 (0)	7 (11.1)	56 (88.9)				<0.005
2000	Manteca	Mechanical	240	123 (51.3)	111	2 (1.8)	16 (14.4)	93 (83.8)				<0.005
2000	Winters	Hand	300	90 (30.0)	87	0 (0)	20 (23.0)	67 (77.0)				<0.005
2000	Winters	Mechanical	200	102 (51.0)	76	1 (1.3)	19 (25.0)	56 (73.7)				<0.005

Table 2. Endocarp strength as measured by force (kg) required to puncture inner endocarp wall at different positions on immature almond fruit 50 d after flowering. (SDs are in parentheses).

Position on inner endocarp circumference (degrees)	Endocarp puncture force (kg)	
	Longitudinal section at and opposite 2° funicular bundle (Peduncle = 0 degrees)	Cross-section at plane of funiculi attachment (Suture = 0 degrees)
	0	NT ^z
10	2.40 (0.23)	0.95 (0.09)
45	2.40 (0.32)	2.54 (0.18)
90	1.69 (0.27)	2.49 (0.18)
135	1.13 (0.18)	2.59 (0.14)
170	1.04 (0.09)	NT
180	NT	2.40 (0.23)
190	2.04 (0.14)	NT
225	2.13 (0.18)	2.40 (0.14)
270	2.09 (0.23)	2.55 (0.27)
315	2.00 (0.18)	2.63 (0.23)
350	1.86 (0.23)	1.18 (0.18)
LSD _{0.05}	0.10	0.12

^z NT = not tested.

Table 3. ANOVA for force required to puncture inner endocarp wall at different positions on the fruit circumference along a) the tangential longitudinal plane at and opposite 2° funicular bundle, and b) along the cross-sectional plane of funiculi attachment.

Source	Longitudinal				
	df	SS	MS	F-value	P-value
Longitudinal position	9	314.33	34.93	173.47	<0.0001
Tree	3	1.61	0.54	2.67	0.06
Position x Tree	27	3.72	0.14	0.68	0.88
Residual	280	56.37	0.2		

Source	Cross-sectional				
	df	SS	MS	F-value	P-value
Cross-sectional position	9	570.66	63.41	225.8	<0.0001
Tree	3	0.62	0.21	0.73	0.53
Position x Tree	27	13.63	0.51	1.8	0.01
Residual	280	78.68	0.28		

Table 4. Endocarp position where probing and feeding by leaffooted bugs was detected by damage to enclosed kernel and seed coat tissue.

<u>Leaffooted bug feeding damage</u>		
Position on inner endocarp circumference <u>(degrees)</u>	Longitudinal section at and opposite 2° funicular bundle <u>(Peduncle = 0 degrees)</u>	Cross-section at plane of funiculi attachment <u>(Suture = 0 degrees)</u>
0	1	1
10	NT ^z	16
45	1	0
90	3	0
115	0	NT
135	5	0
145	2	NT
160	9	NT
180	NT	0
225	0	0
270	0	0
315	0	0
350		4

^zNT = not tested.

In other studies, the chemical identity of key resistance compounds, particularly lignin, is being pursued through a collaborative project with the USDA, Western Regional Research Center in Albany, CA (as part of a USDA aflatoxins elimination project developed to complement this aspect of the breeding program). Disease resistance is also being assessed through evaluation of natural infections in regional plantings of advanced selections and parental lines, and through inclusion in the *Disease Evaluation Block* at UC/Davis being developed by Dr. Jim Adaskaveg from UC/Riverside.

The bulk of field activities for 2001, however, involved the evaluation of approximately 12,000 seedling trees developed from controlled crosses between parents with promising levels of disease resistance and or self compatibility. Achievements in 2001 include (1) the collection of tree and nut data to determine the value of various parental crossing combinations, and (2) the roguing-out or elimination of approximately 70 percent of seedling trees to allow a more detailed quality assessment of remaining crossing progeny in subsequent years.

C. Develop a model for the classification of cropping potential in almond.

Almond cropping potential is determined by multiple factors, including tree architecture, bearing habit, flower density, flower fecundity, and freedom from alternate bearing. Tree architecture and bearing habit are difficult to characterize. An effective classification should accommodate the range in structural forms common to the crop while organizing the structures within intuitive, development-based categories. Although promising advances in modeling shoot growth habit have been reported for pome fruits, particularly apple (*Malus x domestica* Borkh.), the extensive use of winter and summer pruning for stone fruits such as peach (*Prunus persica* (L.) Batsch) and plum (*Prunus salicina* Lindl.) have resulted in limited interest in modeling natural growth habits for these species. Almond is a stone fruit grown for its edible nut that develops laterally on peach-like shoots and perennial spurs. Although closely related to peach, almond trees are not extensively pruned since yield is the main objective. Pruning to increase productivity, including the rejuvenation of older trees, has not been effective because the new bearing wood did not compensate for the older wood removed. Consequently, almond trees develop a wide range of natural architectures. In addition, several native, and structurally variable, *Prunus* species including *P. argentea* (Lam.) Rehd., *P. fenzliana* Fritch., *P. webbii* Spach, *P. tangutica* Batal. and *P. bucharica* Fedtchenko,

grow in Central Asia and Europe. This germplasm has proven a valuable source for disease and insect resistance as well as pollen-pistil self-compatibility. A wide range of tree growth habits results from the hybridization of these species with *P. dulcis*, including the undesirable upright-spindle and bush forms, as well as desirable architectures such as lateral bearing habit. Because of a long juvenile period of 4 or more years for seedling almonds, breeding programs in Spain and California have been evaluating

classifications of early growth habit. Such classifications would be useful for examining the inheritance of different growth habits, as well as the relationship between juvenile and adult tree form. This report describes an almond growth classification that has proven useful in our program and briefly summarizes its application for almond improvement.

Lateral (sylleptic) branching was characterized for current and previous season's growth (Fig. 5). Lateral shoot growth was divided into four categories based on the degree (number) and type of shoot development (spurs vs. shoots). No distinction was made among spurs (up to 5 cm), brindles (5-10 cm) and thorns. Shoots were over 10 cm long. Branching pattern for current season growth was assigned a number from 1 to 4, and branching from 1-year-old growth assigned a letter from a through d, making a unique alpha-numeric code for branching habit (Figs. 5 and 6).

Three crosses were evaluated between parents selected for similar growth habits but showing divergent growth habits in progeny trees. These included the crosses: 'Nonpareil' [growth of 2nd leaf tree designated as '3-c' in Fig. 6] as seed parent crossed with breeding line 'F7,1-1' [4-c], an almond-like tree with *P. persica* in its lineage (Fig. 7); 'D3-6' [3-c] an almond-like tree containing both *P. persica* and *P. webbii* in its lineage crossed with 'F7,1-1' [4-c] as pollen parent; and, 'D3-6' [3-c] x 'Le

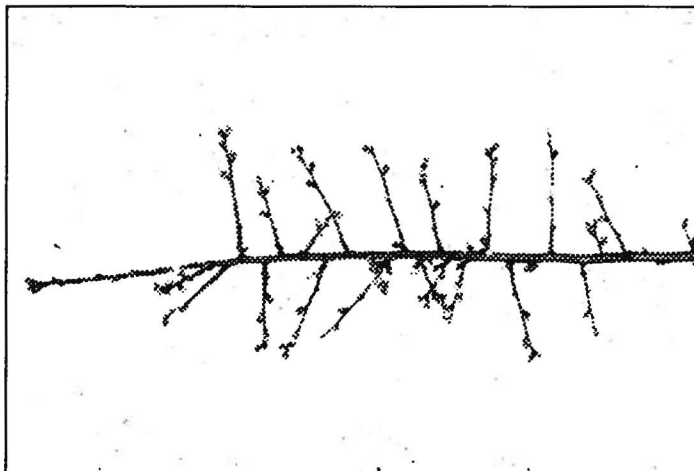


Figure 5. Basic branching patterns observed in almond germplasm with designations based on Figure 6: 1-d for shoot from backcross progeny resulting from *P. dulcis* x *P. webbii* hybrid, showing widespread growth of brindle-type (5-10 cm in length) laterals yet demonstrating the more substantial fruitwood yet continued right-angle orientation to the primary shoot.

Grand' [3-c] a California almond cultivar thought to possess *P. persica* genes as a source of its partial self-compatibility (2). At least 60 progeny from each cross were classified at the end of the third growing season following leaf fall based on the evaluation of the two most vigorous shoots. The distribution of lateral branching ratings of progeny trees was plotted (Fig. 7) using X and Y coordinates based on the lateral branching classification (Fig. 6).

The lateral branching classification (Fig. 6) allowed convenient classification of all growth habits observed in cultivars selections and seedlings. For example, the designation [1-a] describes whip-like growth where all lateral branching is suppressed as occurs in the Spanish cultivar 'Barte'. The designation [1-d] indicates that lateral growth on current season shoots is suppressed but lateral shoots develop profusely on second year wood as often occurs during the early growth of the Spanish cultivar 'Marcona' and many accessions of *P. scoparia*. Branching habits with the designation [4-a] show lateral branching during the first growing season, but limited to no continued growth of those lateral shoots during the second season as is observed in certain hybrids of *P. dulcis* and *P. webbii*. Shoot growth with no lateral suppression for both current and previous seasons [4-d] resulted in a very bushy growth habit characteristic of some *P. tangutica* accessions and their interspecific hybrids.

Growth habits for most commercially acceptable almond types were placed in intermediate categories. For example, 2nd leaf budded trees of 'Nonpareil', the major California cultivar, were characterized as [3-c] as it typically shows limited lateral shoot development on vigorous shoots of both the current and previous season's growth. Laterals typically develop the basal one-half to two-thirds of the shoot or branch (Fig. 3,a), or from the terminal buds of previous season's growth. This branching habit is considered commercially desirable as it results in a moderately branched yet open tree architecture that allows continued terminal fruit-wood production without excessive shading of interior fruit bearing spurs. Crosses using 'Nonpareil' as the seed parent often result in progeny populations skewed towards this [3-c] growth habit, suggesting a high heritability and tendency towards dominance for this trait. The widest range of shoot architectures was in progeny from the cross 'Nonpareil' (3-c) to 'F7,1-1' (4-c). Shoot growth for most progeny from this cross (149 of 245 seedling trees), was characterized as [3-c]. The other branching patterns from this cross occurred at low frequencies. Similar distributions were observed when 'Nonpareil' was used as the pollen parent or in progeny resulting from crosses with other traditional California

cultivars. In the present study, all parents had mature tree, nut, and kernel characteristics within the range generally considered acceptable by the almond industry. Previous research has reported high heritability for growth habit in apple though the genetic variance appeared to be almost entirely additive. The relative uniformity observed in progeny of crosses between California cultivars is not surprising since this germplasm has been reported to be highly inbred with most cultivars having 'Nonpareil' and 'Mission' as parents. This study, however, demonstrates that crosses to dissimilar germplasm can increase variability in progeny growth habit, and parent selection can be employed to skew the population towards desired growth types. The use of 'D,3-6' instead of 'Nonpareil' as seed parent in a cross with 'F7,1-1' produced a population with a distinct skewing towards a bushy [4-d] *P. tangutica*/*P. webbii*-type growth habit. However the cross 'D,3-6' with 'Le Grand' resulted in a population strongly skewed towards a more open [1-c] growth habit.

Shoot growth habit is important not only for determining final tree form but also fruit bearing habit and ultimate cropping potential. Almond fruit are borne primarily on terminal peach-type shoots, sometimes with limited lateral bearing occurring on current season and on previous season wood, as well as on perennial spurs. A significant increase in lateral branching and lateral bearing have been observed in crosses between 'Nonpareil' and *P. webbii* selections. Early backcrosses show greater lateral branching in both current and previous season wood, typically resulting in short, thorn-like or brindle shoots [2-b] with growth occurring at nearly right angles to the stem. One to two additional backcrosses towards commercial almond types often result in a strong lateral bearing habit in current season and/or previous season wood while retaining a unique and desirable right-angle orientation to the stem. Almond cultivars with greater tendency for lateral bearing tend to have more consistent year-to-year tree productivity. The additional bearing surface is thought to buffer against the loss of developing fruit and leaves from disease and environmental stresses. Work in Spain has also shown that promotion of lateral shoots in almond leads to suppression of overly vigorous vegetative growth of terminal shoots, with a greater almond productivity per unit shoot length. The development of lateral branch architectures has become an important breeding objective for walnut (*Juglans regia* L.) owing to its association with high cropping consistency.

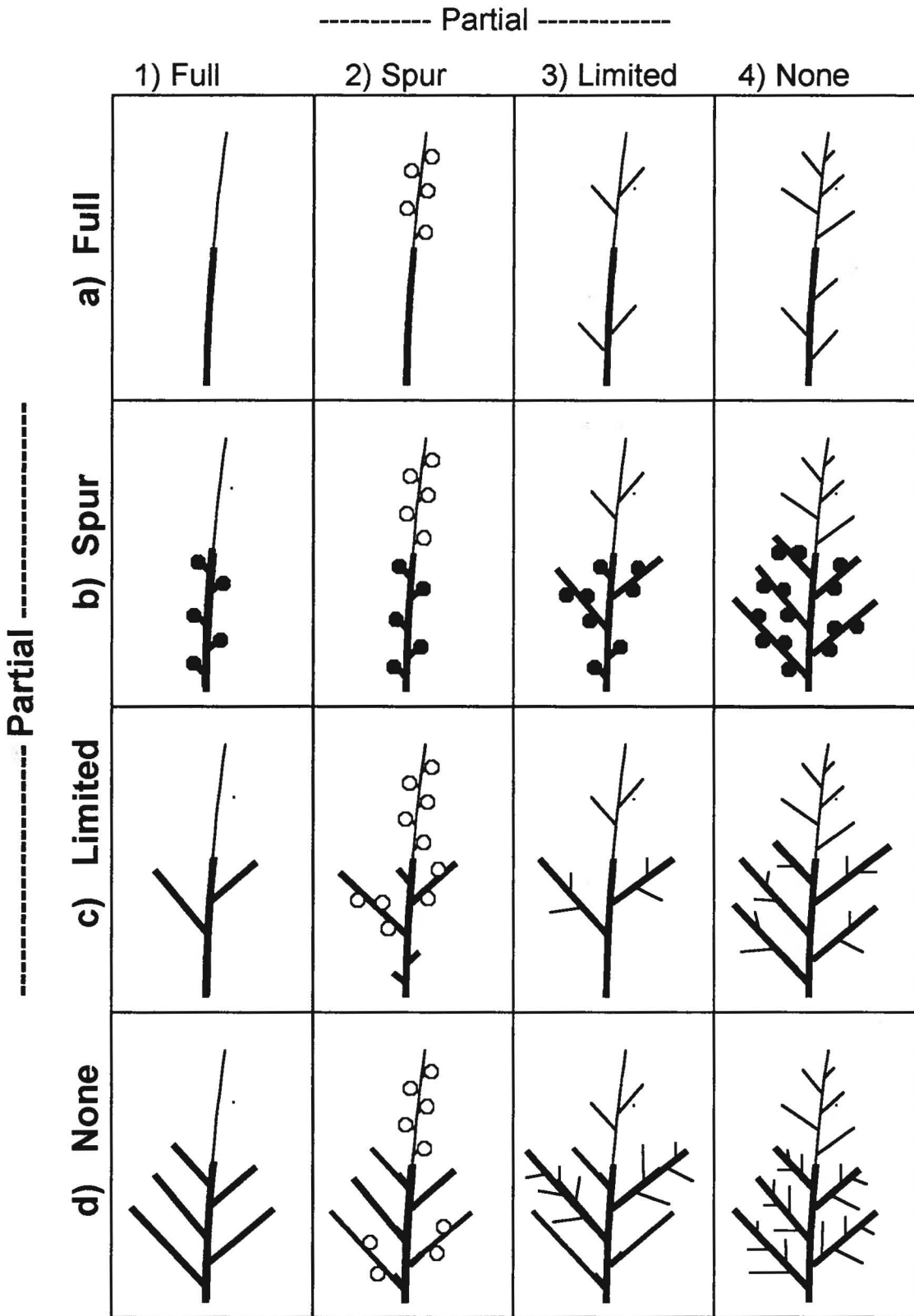
In summary, a lateral branching classification is proving useful in the characterization of almond cultivars as well as breeding populations. Branch architecture classifications have been developed for a range of temperate and tropical tree species. Recent classifications of tree architecture are often based on ontogenetic models where final branch habit is seen as the consequence of “apical dominance” and “apical control”. This developmental approach has provided an effective framework for the classification of the wide range of temperate, tropical and subtropical forest tree species, but becomes more cumbersome for describing differences within a species or related species group due to the wide variability in branching habits possible, as well as differences among researchers in usage of the terms “apical dominance”, “apical control”, and “correlative inhibition”. Our classification simply characterizes the degree and type of lateral branching (Fig. 1) and is not based on hypothetical apical growth responses. In addition to pursuing novel growth habits, the development-based classification is currently being employed as the basis for long-term studies on the relationship of juvenile (seedling) with adult (bearing) tree form in almond.

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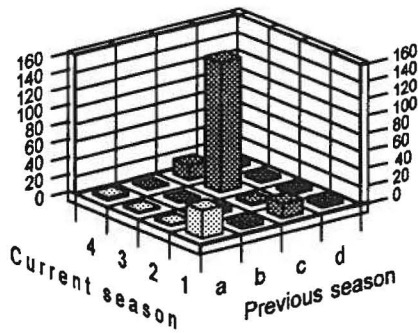
Fig. 6. Chart summarizing the classification of branching patterns based on degree of suppression of lateral shoots in current season and previous season growth.

Suppression of Lateral Shoots on Current Season Growth

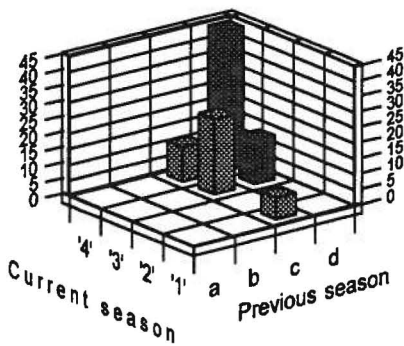
Suppression of Lateral Shoot Growth on Previous Season Wood



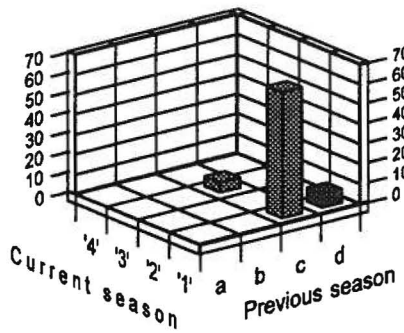
(○-annual spur; ●-perennial spur)



- (a) 'Nonpareil'— F7,1-1 seedling selection
 Sol. Selection 5-15 — Almond seedling
 'Nonpareil' — Selection 22-2
 'Lukens Honey' peach — 'Mission'



- (b) D,3-6 seedling — F7,1-1 (as above)
 F5,4-10 seedling — 'Solano'
 P. webbii — SB6,56-88 seedling
 Sol. selection 5-15 — Selection 24-6
 'Lukens H' peach x 'Mission' ('Nonpareil' x 'Eureka')



- (c) D,3-6 (as above) — 'LeGrand' almond
 (peach in lineage?)

Figure 7. Parentage and branch architecture distribution of three-year-old own-rooted progeny trees based on the classification in Fig. 6.